ECOLOGY AND BEHAVIOR

Early-Season Colonization Patterns of the Boll Weevil (Coleoptera: Curculionidae) in Central Texas Cotton

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ABSTRACT It is commonly believed that colonization of early-season cotton, Gossypium hirsutum L., by overwintered boll weevils, Anthonomus grandis grandis Boheman, is concentrated on field margins. However, supporting experimental evidence is not available. In 1999 and 2000, we examined colonization patterns of overwintered boll weevils in Central Texas cotton on the bases of adult collections by a pneumatic sampler and hand collections of abscised infested squares. Samples were taken from sites arranged in a grid that extended inward >70 m from the field margin. Adults were collected from shortly after seedling emergence until the flowering stage, and infested squares were collected during the one-third grown square stage. Despite numerical trends, the numbers of adult weevils collected were not significantly different between years or sexes, or among plant phenological stages. Field-to-field variation among collections was considerable and likely prevented detection of differences among these factors. Spatial patterns represented by adult weevil and infested square collections were examined by logistic regressions fitted to the respective probabilities of weevil detection at each designated sample site. Although we observed trends for slightly decreased probability of weevil detection with increased distance from the field margin, these trends were too weak to be demonstrated statistically. Our results indicate the boll weevil does not consistently exhibit a strong edge-oriented colonization pattern, and that management tactics that are predicated on these patterns, such as border sprays, should be used with caution.

KEY WORDS boll weevil, Anthonomus grandis grandis, colonization, cotton

COTTON PRODUCERS IN MANY areas of Texas routinely use 1-5 early-season insecticide applications to reduce populations of overwintered boll weevils (Anthonomus grandis grandis Boheman) in cotton, Gossypium hirsutum L. This early-season approach to boll weevil management was promoted in Texas by Armstrong et al. (1980), and has become an integral part of most boll weevil eradication programs (Allen 2001). However, concern for the disruption of beneficial arthropod populations and consequent release of secondary pests (Summy et al. 1996), high insecticide costs, and potential environmental risks, has in some cases prompted the use of border sprays in the place of whole-field treatments. In the border spray approach, only field margins are treated in hopes of maintaining a refuge of beneficial arthropods in field interiors and reducing the amount of applied insecticide. However, the use of this approach presumes the presence of a pronounced edge-oriented colonization pattern by overwintered weevils.

While it is widely recognized that boll weevils initially colonize field margins, such colonization patterns have not been experimentally demonstrated. Little and Martin (1942) reported that initial boll wee-

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vil damage occurs at the field edge and subsequently spreads throughout the field as food resources become scarce, although they provided no supporting data. Based on trap captures, Guerra (1986) also suggested that boll weevils initially colonize field margins. However, his use of grandlure-baited traps may have influenced observed colonization patterns. In contrast, Hixson (1936) examined the distribution of adult boll weevils within a field in Oklahoma and found higher numbers of weevils near the center of the field than near the edges. An improved understanding of colonization patterns will be essential in assessing the value of border sprays for early-season boll weevil management. Our objective was to examine earlyseason boll weevil colonization patterns in Central Texas cotton based on spatial and temporal patterns of collections of adults and fallen infested squares.

Materials and Methods

Experimental Design. Study arenas were established in commercial cotton in Burleson and Robertson counties, TX, in 1999 and 2000. Three fields were sampled in 1999 ('Deltapine 5557' planted 8 April and 'Bt 20' planted 23 April to two fields). Two study arenas were established on opposite sides of one field,

and the other two fields each contained a single study arena. In 2000, three fields planted to 'Deltapine 5690' on 21 April, and one field planted to 'Deltapine 5415' on 18 April, were sampled. The field planted 18 April was partially replanted on 10 May because of stand loss to hail. One field contained two study arenas on opposite sides while remaining fields each contained a single study arena. Fields sampled in both years ranged in size from ≈3-100 ha.

Each study arena consisted of the outermost 71 rows (1.02-m row spacing) on one side of a field. Within each study arena, seven sets of three rows each were designated for sampling (rows 1–3, 6–8, 12–14, 18–20, 29–31, 49–51, 69–71, respectively). The 3-row sets were unequally spaced to provide the highest resolution of a colonization gradient nearest the field margin. Within each 3-row set, three 50-m sections of row were delineated; one at each end of a row (row end) and one spanning the midpoint of the length of row (row length middle). Each 50-m section was further divided into 10-m subsections to improve resolution of a colonization gradient down the row. Thus, each sample arena was comprised of 21 50-m sections, each further divided into five 10-m subsections.

On each sample date, one row from each 3-row set was sampled. Rows were randomly selected without replacement until all rows in each respective 3-row set had been sampled. Sampling was alternated among rows within row sets to minimize damage to plants from repetitive sampling.

Most fields received one or more insecticide treatments during the study period. In 1999, one field was treated a total of three times, including a treatment of acephate before the appearance of fruit and one treatment each of dicrotophos and carbofuran after onethirds-grown squares (>6 mm diameter) were present. Also, one field containing two sample arenas was treated twice, including a treatment of dicrotophos during the matchhead square (3-6 mm diameter) stage and one of carbofuran after one-thirdgrown squares were present. One field was not treated. Treated fields were sampled within 3-6 d of insecticide application, and where multiple insecticide treatments were applied they were separated by 6-8 d. In 2000, one field was treated once with dicrotophos during the matchhead square stage, two fields containing a total of three sample arenas were treated twice (dicrotophos applied during the matchhead square stage in two sample arenas and during the one-third-grown square stage in one arena; endosulfan in both fields after one-third-grown squares were present), and the remaining field was not treated. Fields were sampled within 1-5 d of insecticide application and multiple applications were separated by 12 d. All treatments in both years were applied by ground equipment. In two of the four arenas sampled in 1999, and four of the five arenas sampled in 2000, 4-7samples were collected before the first insecticide application.

Adult Collections. In 1999 and 2000, adult weevils were collected using a modified leaf blower (KISS; Beerwinkle et al. 1997). Sampling was initiated when

plants were 10–15 cm in height and had 2–6 true leaves. Adults were collected from each sample arena twice weekly until shortly after one-third grown squares were present, and weekly thereafter until the initiation of flowering. Contents of the KISS collection net were removed at the end of each 10-m subsection, placed into a sealable plastic bag, and labeled according to date, sample arena, 3-row set, 50-m section, and 10-m subsection. All samples were transported to the laboratory where adult weevils were counted and sexed using the method of Sappington and Spurgeon (2000).

Fallen Square Collections. Population levels of overwintered boll weevils colonizing early-season cotton are normally too low to facilitate collection of substantial numbers of weevils. However, each female boll weevil deposits a comparatively large number of eggs, the locations of which can serve as temporary indicators of weevil presence. We sampled fallen oviposition-punctured squares in an effort to obtain improved estimates of weevil distribution patterns in the case that adult population levels were inadequate for this purpose.

Fallen squares were collected weekly in 2000, beginning when they were first apparent in furrows, and from the same sample arenas as adults. Sampling continued until the initiation of flowering. Fallen squares were repeatedly collected from the same furrow within each 3-row set each week. Collected squares were placed in sealable plastic bags labeled according to date, sample arena, 3-row set, 50-m section, and 10-m subsection. All samples were transported to the laboratory for processing. Squares lacking the nipple-like protrusion that indicates a sealed oviposition puncture were considered uninfested and were discarded. Remaining squares were dissected to confirm infestation. Only squares containing weevils were included in subsequent analyses.

Plant Phenology. Plant development was monitored by examining two randomly selected plants from near each 50-m section on each sample date (42 plants per sample arena). Plants not yet producing fruit were classified as prefruiting. When fruit were present, plant phenological stage was based on presence of pinhead squares (square diameter <3 mm), matchhead squares (>3-6 mm square diameter), and one-third grown squares (square diameter >6 mm). The most mature fruit detected within a sample arena was used to characterize the plant phenological stage of a given sample arena from that date forward until a more mature fruit was detected.

Statistical Analyses. Previous reports indicate that boll weevil colonization markedly increases at the onset of fruiting (Walker and Bottrell 1970, Roach et al. 1971, White and Rummel 1978). Further, presence of male boll weevils may influence colonization patterns through the production of a pheromone that attracts both sexes (Keller et al. 1964, Hardee et al. 1969). Therefore, the influences of year, plant phenology, weevil sex, and interactions of these main effects on the numbers of weevils collected in a sample arena were assessed by analysis of variance (ANOVA)

(PROC GLM; SAS Institute 1988). The total numbers of adult weevils collected from each sample arena on each date were used in the analyses because the numbers of weevils collected in each 10-m subsection or 50-m section were typically low and most counts were zero. Thus, in this analysis, the sample arena was the experimental unit.

Because sample areas located on field ends were subject to colonization gradients from two directions (across rows, down rows) while sample areas located in row length middles were only subject to a colonization gradient across rows, colonization patterns for row ends and row length middles were examined separately. Also, because the presence of fruit influences weevil behavior (Mitchell and Mistric 1965), pheromone production (Keller et al. 1964, Hardee et al. 1969), and the efficiency of pneumatic samplers (Raulston et al. 1998), and because more advanced stages of plant development occur later in the period of weevil emergence from overwintering, colonization patterns were examined separately for each plant phenological stage (prefruiting, pinhead square, matchhead square, and one-third grown square).

The low numbers of adult weevils collected from respective 10-m row subsections on most sample dates, and the fact that 87% of samples were characterized by zero counts precluded examination of colonization patterns in relation to distance from the field margins by ANOVA or multiple regression procedures. Instead, because 97.4% of all counts were zeros or ones, counts from individual 10-m subsections (row ends) or 50-m sections (row length middles) were converted to a binomial form by considering only whether weevils were present (1) or absent (0) in a given sample. Samples from different sample arenas were then combined according to plant phenological stage so that the proportion of samples at a given location (3-row set and either 10-m subsection or 50-m section) containing one or more weevils represented an estimate of the probability that a weevil would be detected at that location. If the boll weevil preferentially colonizes field margins, the probability of weevil presence should decrease with increasing distance from the field margin either across or down the rows. The converted data were examined for such a pattern by logistic regression (PROC LOGISTIC, SAS Institute 1988).

Logistic regressions examining the relationship between the probability of weevil presence and distance from the field margin at row ends were of the form $Y = 1/[1 + e^{-(\beta_0 + \beta_1*ROWSET + \beta_2*SUBSECTION + \beta_3*ROWSET*}]$, where Y is the probability of collecting a weevil at a given location, ROW SET is the distance in rows from the field margin of the midpoint of a 3-row set, SUBSECTION is the distance in m of the innermost end of a 10-m subsection from the row end, ROW SET*SUBSECTION represents the row set by subsection interaction, and β_0 , β_1 , β_2 , and β_3 are estimated. Presence of a statistically significant relationship between 10-m subsection location and the probability of detecting a weevil was assessed using the Wald χ^2 (SAS Institute 1988). Analyses for row length middles

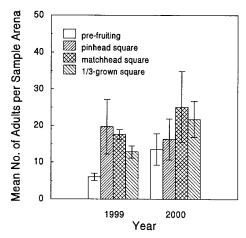


Fig. 1. Population estimates (\pm SE) of adult boll weevils based on KISS samples of 1050 m of row in cotton at four plant phenological stages, Brazos Valley, TX, 1999 and 2000.

were identical to those for row ends except the model contained only the intercept (β_0) and row set (β_1) terms, and proportions of samples containing weevils were calculated on the basis of the entire 50-m section of row instead of individual 10-m subsections.

Counts of fallen infested squares were analyzed using the same procedures applied to adult counts from KISS collections. In these analyses, the logistic model was fitted to the respective probabilities of the presence of one or more infested squares containing any weevil life stage in each sample location. Because fallen infested squares were collected only during the one-third grown square stage, only two analyses (row ends and row length middles) were conducted.

Results and Discussion

Numerical differences in the mean numbers of weevils collected per sample arena (1050 m of row) were apparent between years (mean \pm SE; 1999, 13.8 \pm 1.47 weevils; 2000, 19.8 ± 3.16 weevils), weevil sexes (male, 10.2 ± 1.24 weevils; female, 6.9 ± 0.84 weevils), and stages of plant phenology (Fig. 1). However, the overall ANOVA in which these effects were examined was not statistically significant (F = 1.40; df = 15, 96; P =0.16). Lack of significant differences in the numbers of weevils between years and sexes was probably a product of the considerable field-to-field variation in weevil population levels. In addition, early-season insecticide applications may have minimized population differences between years. Similarly, differences in weevil population levels among stages of plant phenology were likely minimized by insecticide treatments because treatments were only applied to fruiting stages which contained numerically higher weevil population levels. Raulston et al. (1998) indicated that the presence of fruit on cotton plants was associated with a decline in the efficiency with which adult boll weevils were collected by a pneumatic sampler. Thus, differences in weevil population levels among plant

Table 1. Regression coefficients for logistic regressions fitted to the probability of adult boll weevil presence in 10-m subsections arranged across and down rows on row ends of cotton at four stages of plant phenology

Plant phenology		Model parameters ^a (SE)					
	Intercept	$\mathrm{Row}\;\mathrm{set}^b$	${\bf Subsection}^c$	Row set by subsection interaction	Wald χ^2	df	P
Prefruiting	-2.336 (0.442)	-0.001 (0.013)	0.079 (0.130)	-0.001 (0.004)	0.90	3	0.83
Pinhead square	-1.075(0.451)	-0.024 (0.015)	-0.210(0.143)	0.006 (0.004)	3.29	3	0.35
Matchhead square	-1.709(0.339)	-0.0004 (0.0097)	0.056 (0.101)	-0.001 (0.003)	0.69	3	0.88
1/3-grown square	-1.478(0.239)	$-0.003\ (0.007)$	-0.112(0.076)	0.0002 (0.0022)	5.46	3	0.14

^a Logistic model was $Y = 1/[1 + e^{-(\beta_0 + \beta_1*ROW SET + \beta_2*SUBSECTION + \beta_3*ROW SET*SUBSECTION)}]$, where Y is the probability of weevil detection.

phenological stages may have been further obscured by a decrease in collection efficiency of the KISS with increasing plant development.

Walker and Bottrell (1970), Roach et al. (1971), and White and Rummel (1978) indicated that colonization of overwintered weevils was coincident with the onset of fruiting. However, we collected considerable numbers of adult weevils before the occurrence of matchhead or one-third grown squares (Fig. 1). Our results indicate that colonization by overwintered weevils begins before fruit are available in the field.

Considerable variation was observed in the distributions of weevils among individual fields and sample dates. Thus, logistic regressions applied to data from row ends did not indicate a significant relationship between the probability of collecting a boll weevil and distance from the field margin, either across rows or down row lengths (Table 1). In fact, a larger total number of weevils were collected from the 3-row set centered on row 70 than from that centered on row two during both the pinhead and matchhead stages of plant development. Further, the 10-m subsections located most distant from the field margin accounted for the lowest number of weevils captured (32) only during the matchhead square stage, when a total of 37 weevils were captured from the subsections adjoining the field margin. Although these summaries illustrate the apparent weakness of any colonization gradient that may have been present, they do not adequately reflect the pronounced variability in the distributions of weevils among individual samples.

Similar analyses of weevil counts from the middle sections of row lengths also failed to indicate a statistically significant relationship between weevil occurrence and distance from the field margin (Table 2). The forms of some of the fitted logistic models indicated the probability of collecting a boll weevil tended to decrease slightly with increasing distance from the field margin. For instance, in the regression for counts from row length middles at the one-third grown square stage, the predicted probability of collecting a weevil decreased from 0.14 in the second row to 0.10 in row 70. However, 9.9% of the total weevils captured (10.9% of nonzero counts) were collected from the 3-row set centered on row 70, and the highest percentage of weevils (20.4%; 18.5% of nonzero counts) were captured from the row set centered on row 7. Overall, the most distant row set yielded the lowest percentage of total weevils captured only during the one-third grown square stage, and the row set nearest the field margin yielded the highest percentage of weevils captured only during the matchhead square stage. Further, the extent of variation in the distributions of weevils among fields and sample dates was similar to that observed for field ends. Thus, any relationships between weevil presence and distance from the field margin that may have been present were either too weak or too variable among fields to be demonstrated statistically.

Results from the logistic regressions applied to fallen square data were similar to those applied to adult collections, for both row ends and row length middles (Table 3). That the collections of fallen squares did not reveal a spatial gradient dependent on distance from the field margin was not unexpected because these collections were anticipated to serve as an amplification of the numbers observed in the adult collections. However, it is uncertain if the square collections provided information that accurately reflected adult colonization patterns because no pattern

Table 2. Regression coefficients for logistic regressions fitted to the probability of adult boll weevil presence in 50-m sections arranged across rows near the middle of row lengths of cotton at four stages of plant phenology

Dl. a d. a d. a	Model parar	meters ^a (SE)	xx 11 2	16		
Plant phenology	Intercept	Row set ^b	Wald χ^2	df	P	
Prefruiting	-2.255 (0.297)	-0.015 (0.010)	2.25	1	0.13	
Pinhead square	-2.029(0.324)	-0.007(0.010)	0.56	1	0.46	
Matchhead square	-1.557(0.211)	-0.010(0.007)	2.28	1	0.13	
1/3-grown square	$-1.713\ (0.149)$	-0.007(0.005)	2.40	1	0.12	

^a Logistic model was $Y = 1/[1 + e^{-(\beta_0 + \beta_1 * ROW SET)}]$, where Y is the probability of weevil detection.

^b Row set is the distance in rows from the field margin of the midpoint of a 3-row set.

^c Subsection represents the distance from the field margin down the row length in 10-m increments.

^b Row set is the distance in rows from the field margin of the midpoint of a 3-row set.

Table 3. Regression coefficients for logistic regressions fitted to the probability of the presence of fallen boll weevil-infested squares in row sections arranged across and down rows in cotton at the one-third grown square stage

		Model parameters ^a (SE)					
Section location	Intercept	Row set ^b	$Subsection^c$	Row set by subsection interaction	Wald χ^2	df	P
Row ends Row length middles	-0.264 (0.268) -0.549 (0.164)	-0.002 (0.007) 0.0004 (0.0046)	-0.006 (0.008) -	0.0001 (0.0002)	1.24 0.01	3 1	0.74 0.92

[&]quot;Logistic model for row ends was $Y=1/[1+e^{-(\beta_0+\beta_1*ROW\,SET+\beta_2*SUBSECTION+\beta_0*ROW\,SET*SUBSECTION)}]$, and logistic model for row length middles was $Y=1/[1+e^{-(\beta_0+\beta_1*ROW\,SET)}]$, where Y is the probability that one or more infested squares will be detected.

in adult collections was observed for comparison, and presence of fallen infested squares on a given date was limited to areas of the field where squares were present. Nevertheless, these collections indicated the presence of substantial numbers of infested squares regardless of distance from the field border.

Hixson (1936) provides the only other published study of boll weevil colonization pattern based on sampling of adults from different areas of the field. Although the results of Hixson (1936) did not indicate a pattern of weevil presence that was biased toward field edges, that study was neither replicated nor statistically analyzed. Regardless, our findings are consistent with those of Hixson (1936) in that we also failed to detect an edge-biased pattern in weevil colonization.

Our results challenge the widely accepted notion that early-season boll weevil colonization occurs primarily on field margins. Although some analyses showed a slight trend for a reduced incidence of weevil occurrence with increasing distance from the field margin, these patterns were not representative of most samples and could not be demonstrated statistically. More importantly, when such patterns were suggested, weevils remained relatively abundant at sites distant from the field edge. Given the observed general distribution of weevils throughout the sample arenas, early-season border sprays and other control tactics predicated on an edge-oriented colonization pattern would seem unlikely to supply effective control. Our findings suggest that sole reliance on such tactics would risk leaving a substantial and potentially damaging reservoir of colonizing weevils in the field interior.

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^b Row set is the distance in rows from the field margin of the midpoint of a 3-row set.

^c Subsection represents the distance from the field margin down the row in 10-m increments.

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